Visuo-proprioceptive recalibration and the sensorimotor map

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35 **ABSTRACT**

36 Spatial perception of our hand is closely linked to our ability to move the hand accurately. We might

37 therefore expect that reach planning would take into account any changes in perceived hand position; in

38 other words, that perception and action relating to the hand should depend on a common sensorimotor

39 map. However, there is evidence to suggest that changes in perceived hand position affect a body

40 representation that functions separately from the body representation used to control movement. Here

41 we examined target-directed reaching before and after participants either did (Mismatch group) or did

42 not (Veridical group) experience a cue conflict known to elicit recalibration in perceived hand position.

43 For the reaching task, participants grasped a robotic manipulandum that positioned their unseen hand

44 for each trial. Participants then briskly moved the handle straight ahead to a visual target, receiving no

45 performance feedback. For the perceptual calibration task, participants estimated the locations of

46 visual, proprioceptive, or combined cues about their unseen hand. The Mismatch group experienced a

47 gradual 70 mm forward mismatch between visual and proprioceptive cues, resulting in forward

48 proprioceptive recalibration. Participants made significantly shorter reaches after this manipulation,

49 consistent with feeling their hand to be further forward than it was, but reaching performance returned

50 to baseline levels after only 10 reaches. The Veridical group, after exposure to veridically-aligned visual

51 and proprioceptive cues about the hand, showed no change in reach distance. These results suggest that

52 perceptual recalibration affects the same sensorimotor map that is used to plan target-directed reaches.

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54 **KEYWORDS**

55 Reaching, sensorimotor map, recalibration, proprioception, hand

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58 **NEW & NOTEWORTHY**

59 If perceived hand position changes, we might assume this affects the sensorimotor map and, in turn,

60 reaches made with that hand. However, there is evidence for separate body representations involved in

61   perception vs. action. After a cross-sensory conflict that results in proprioceptive recalibration in the

62   forward direction, participants made shorter reaches as predicted, but only briefly. This suggests

63   perceptual recalibration does affect the sensorimotor map used to plan reaches, but the interaction

64   may be short-lived.

65

66   **1.   INTRODUCTION**

67   To plan and execute hand movements to interact efficiently with objects in the environment, the brain

68   must have an accurate representation of the hand's position. This representation is thought to be

69   multisensory, including both visual information from the eyes and proprioceptive information from the

70   muscles and joints of the upper limb (1). When both a visual estimate (h_V) and a proprioceptive estimate

71   (h_P) of true hand position (H) are available, these are weighted and combined to form a single integrated

72   estimate (h_{VP}):

73 $$h_{VP} = w_V h_V + (1 - w_V) h_P \tag{1}$$

74   where w_V is the weight of vision relative to proprioception (i.e., w_V = 0.7 implies 70% reliance on vision

75   and 30% reliance on proprioception). Weighting may be determined by relative variance in the sensory

76   signals (1–3) as well as top-down influences such as attention or task demands (4,5).

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78   h_V and h_P do not agree perfectly even in normal circumstances (6), but in the presence of an externally-

79   imposed conflict between these cues, visuo-proprioceptive recalibration occurs (7–9). This may involve

80   both a shift of the proprioceptive estimate closer to the visual estimate (Δh_P), and vice versa (Δh_V).

81   Proprioceptive recalibration can be conceptualized as perceiving the endpoint effector (hand) to be

82   closer to a visual cue than it is in reality; in other words, a high-level change in bodily perception. This

83   does not necessarily imply a change in the lower-level proprioceptive signals about arm configuration.

84   Indeed, we recently found evidence that proprioceptive recalibration is somatotopically focal (10): when

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85 visual cues of fingertip position are shifted forward from proprioceptive cues, the fingertip feels as

86 though it has shifted further away from the body. The knuckle was also felt to be forward-shifted to a

87 lesser extent, but wrist and elbow perception did not show any evidence of a shift (10). In other words,

88 when induced this way, "proprioceptive recalibration" is really a localized distortion in the high-level

89 proprioceptively-derived representation of fingertip position that is evident when only somatosensory

90 cues are available.

91 We might expect that reach planning would take into account any such changes in perceived hand

92 position; in other words, that perception and action relating to the hand should depend on a common

93 sensorimotor map. We recently observed somatotopically-focal changes in the excitability of primary

94 motor cortex (M1) that were specifically related to visuo-proprioceptive recalibration, after controlling

95 for motor behavior (10,11); findings like these are suggestive of a close relationship between perception

96 of hand position and motor execution involving that hand. However, substantial work has suggested

97 that changes in perceived hand position may affect a body representation that functions separately

98 from the body representation used to control movement; these have been referred to as the body

99 image and body schema, respectively (12–14).

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101 Literature addressing some form of visuo-proprioceptive recalibration is mixed as to whether movement

102 is affected. One challenge is the lack of research specifically focused on visuo-proprioceptive

103 recalibration, unconfounded by other processes that are often the primary focus. For example, there is

104 relevant literature using the Rubber Hand Illusion (RHI), a paradigm that creates illusory body ownership

105 over a fake arm through synchronous stroking of the seen fake arm and the hidden real arm (15). The

106 RHI in a sense involves a visuo-proprioceptive cue conflict, since the fake arm is meant to be a visual cue

107 related to the real arm, and proprioceptive recalibration (described as drift in this literature) is thought

108 to occur (16,17). Kammers et al. (2009) concluded that the RHI affected the body image but not the

109   body schema, after observing that perceptual judgments, but not ballistic motor responses, were

110   sensitive to the RHI. On the other hand, in the original RHI study by Botvinick and Cohen (1998), the

111   illusion was assessed by having participants point at the perceived location of their other hand, a motor

112   response that clearly *was* affected by the RHI (12,15). A complication is that in both studies, the pointing

113   movements (15) and ballistic movements (12) were directed toward the other hand, potentially causing

114   participants to access both body schema and body image.

115

116   A second relevant body of literature is the subset of visuomotor adaptation research that measures

117   proprioceptive recalibration. Visuomotor adaptation is a cerebellum-dependent process in which

118   participants experience a systematic perturbation of their movements and gradually compensate by

119   updating their sensorimotor map to reduce systematic errors (18,19). A common method of

120   perturbation is cursor rotation, where participants move their unseen hand to guide a cursor to a target

121   on a screen. The cursor can be rotated; e.g., a movement straight ahead results in the cursor moving

122   30° to the right. In addition to causing movement errors that lead to updating of motor commands, the

123   mismatch between hand and cursor creates a visuo-proprioceptive conflict. Indeed, proprioceptive

124   recalibration has now been documented extensively in this paradigm (8,20,21).

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126   Several studies have used a modified cursor rotation paradigm to eliminate the motor adaptation

127   aspect: participants move their hand along a set channel that gradually deviates from the cursor, which

128   always moves to the target so that no movement error is apparent but the visuo-proprioceptive

129   mismatch is still created (22–24). Participants indeed recalibrate proprioception in these circumstances,

130   and additionally, target-directed reaches with no cursor show a shift in direction consistent with the

131   change in felt hand movement direction (22–24).

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133   It makes sense that a visuo-proprioceptive mismatch created in the context of cursor rotation, with the

134   hand actively or passively moved in a direction rotated from the cursor and target, would alter the same

135   sensorimotor map used to plan target-directed reaches. However, it is difficult to generalize this finding

136   to visuo-proprioceptive recalibration in general, which does not require either active or passive

137   movement, or a movement target. In the cursor rotation paradigm, the cue conflict exists only in the

138   context of target-directed movement: the conflict changes from zero at the home position to some

139   maximum angular deviation at the target position.

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141   Here we ask a slightly different question: Does visuo-proprioceptive recalibration, triggered with a cue

142   conflict at a static position, affect the same sensorimotor map used to make active target-directed

143   reaching movements? Or does it affect a separate body representation, as in the body image vs. body

144   schema concept? To answer this question, two groups of participants made straight-ahead target-

145   directed reaches, with no cursor, before and after experiencing either a visuo-proprioceptive conflict

146   (Mismatch group) or veridical visuo-proprioceptive cues (Veridical group) while the hand was stationary.

147   The cue conflict was introduced by gradually shifting the visual cue forward from the hand, to a

148   maximum of 70 mm (Fig. 1). Proprioceptive recalibration was thus expected in the forward direction

149   (Fig. 1Bii). We therefore predicted that the Mismatch group, feeling the hand to be further forward than

150   it really was after proprioceptive recalibration, would make shorter reaches after experiencing the

151   conflict (Fig. 1Ci-ii), while Veridical group reach distance would remain unchanged.

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156   **2.   METHODS**

157   **Participants**

158   32 healthy right-handed adults participated in the study, which consisted of one lab visit. Inclusion

159   criteria were: aged 18-45 and right handed with normal or corrected-to-normal vision. Exclusion criteria

160   were any muscular, orthopedic, or neurological disorders. All enrolled participants reported that they

161   met these inclusion and exclusion criteria. The study was approved by Indiana University Institutional

162   Review Board, and all participants gave written informed consent. Participants were randomly assigned

163   to the Mismatch group (N = 16, mean age 19.9 ± SD 1.2 years, 4 males) or the Veridical group (N = 16,

164   mean age 20.5 ± 1.8 years, 6 males) using a random sequence of ones and twos (16 of each) generated

165   in MATLAB 2021a (Mathworks). The study was single blind, with the experimenter knowing the

166   participant's group assignment but the participant not knowing.

167

168   **Apparatus**

169   Participants were seated at a reflected rear projection apparatus to perform a task with three parts (Fig.

170   1), grasping the handle of a KINARM Endpoint 2D robotic manipulandum (BKIN) with their right hand

171   throughout. Positional accuracy of the manipulandum, with high-resolution secondary encoders, is 3

172   microns; inertial load of the passive manipulandum is 0.8/1.0 kg (minor/major axes). Participants had no

173   direct vision of their hand, but viewed a task display that appeared to be in the plane of the

174   manipulandum (Fig. 1A).

175

176   **Procedures**

177   The experimental session consisted of three parts. First, pre-calibration straight-ahead right-hand

178   reaches to a visual target with no visual feedback about the right hand (Fig. 1A). Second, a visuo-

179   proprioceptive calibration task with either mismatched or veridical visual and proprioceptive cues about

180   the right hand, depending on group assignment (Fig. 1B). Third, post-calibration straight-ahead right-

181   handed reaches to a visual target with no visual feedback about the right hand (Fig. 1C). The experiment

182   was preceded by instructions about the two tasks (reaching and calibration) and practice of each task.

183   The whole session took about one hour.

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186   *Straight-ahead reaching.* Before and after the visuo-proprioceptive calibration task (Fig. 1A and C),

187   participants were asked to grasp the manipulandum handle in their right hand and briskly move from

188   the starting position to the target. The hand was brought passively to the starting position for each trial,

189   as the starting position was not visible. No online or endpoint visual feedback about hand position was

190   given at any point in this task. Reach endpoint was defined as the position at which movement velocity

191   dropped below 5% of peak velocity.

192   In addition to practice trials, participants performed 20 reaches pre-calibration and 20 reaches post-

193   calibration. The starting position was located at the participant's body midline, about 20 cm in front of

194   their chest. The visual target was located 10 cm forward of the starting position.

195   Reaches were binned into sets of 5. To determine if reach endpoints were closer or further from the

196   participant after the calibration task, the y-coordinates of each set of 5 reach endpoints were averaged

197   within participants.

198   *Visuo-proprioceptive calibration task.* Visuo-proprioceptive estimates of hand position are most

199   commonly measured and/or perturbed with a bimanual task, using an "indicator" (left) hand to indicate

200   the participant's perception of the "target" (right) hand's position when visual, proprioceptive, or both

201   types of information about the target are available (2,6,25–27). Participants were therefore asked to use

202   their *unseen left index finger* to indicate on a 32 inch touchscreen (PQLabs) where they perceived a

203   series of targets (Table 1) related to the *right (target) hand* (Fig. 1B)*,* which grasped a stationary

204   manipulandum handle at the target position beneath the touchscreen. It was not physically possible to

205   place the touchscreen in the horizontal plane of the visual task display at the top of the manipulandum

206   handle, due to the design of the manipulandum. Therefore for this task we moved the actual

207   manipulandum out of the workspace and placed a replica manipulandum handle under the touchscreen

208   for participants to grasp on P and VP targets. The replica was the same height and diameter as the real

209   handle, and covered with an identical rubber grip.

Table 1. Targets in visuo-proprioceptive calibration task.

Visuo-proprio (VP) target	Participant grasped stationary manipulandum handle in the <u>right hand</u> beneath the touchscreen. A white disc appeared to be at the top of the handle. Participant was signaled to move the *unseen* left indicator finger, on the upper side of the touchscreen, from one of five start positions to where he perceived the VP target to be.
Proprioceptive (P) target	Identical to the VP target except no white disc. Participant was asked to indicate where he perceived the center of the handle as accurately as possible by placing the unseen indicator finger at that position.
Visual (V) target	The white disc was displayed at the target position, but the right hand was down at the participant's side. Participant was asked to move his unseen indicator finger to where he perceived the white disc.

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211   Both groups performed 84 trials: 42 VP, 21 V, and 21 P, in repeating order (VP-V-VP-P). For the Veridical

212   group, the white disc was always displayed veridically at the top of the replica manipulandum handle.

213   For the Mismatch group, the white disc moved 1.67mm forward on each VP trial. Participants do not

214   generally notice this perturbation, which results in a 70mm visuo-proprioceptive mismatch by the end of

215   the 84 trials (Fig. 1Bii) (7,28–30). Indicator finger start position was jittered to prevent participants from

216   being influenced by indicator finger movements on the previous trial. Importantly, there was no speed

217   requirement and no performance feedback or knowledge of results, to preclude motor adaptation.

218

219   If the proprioceptive estimate of the right hand, as shown by left indicator finger endpoints, moves

220   forward to close the visuo-proprioceptive gap (Δh_P), then we observe overshoot on P targets. Similarly, if

221   perceived position of the white disc moves closer to the right hand (Δh_V), then we observe undershoot

222   on V targets. *VP trials are used to create the mismatch while V and P trials are used to assess visual and*

223   *proprioceptive recalibration*. Thus, outcome measures are based on V and P trials. We quantified visual

224   and proprioceptive recalibration (Δh_V and Δh_P) as previously (28–30): after calculating mean indicator

225   finger endpoint positions in the y-dimension on the first and last 4 V and P trials, respectively, we

226   computed the difference relative to actual target position, which was constant for P targets but shifts

227   70mm for V targets (Mismatch group only):

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229    $$\Delta h_P = last\ 4\ P\ endpoints - first\ 4\ P\ endpoints \qquad\qquad (2)$$

230

231    $$\Delta h_V = 70 - (last\ 4\ V\ endpoints - first\ 4\ V\ endpoints) \qquad\qquad (3)$$

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234   **Statistical analysis**

235   Data were processed using MATLAB 2021a (MathWorks Inc., Natick, MA, United States). A mixed model

236   ANOVA was performed on the straight-ahead reaching endpoints, with within-participant factor "reach

237   set" (the last set of 5 pre-calibration reach endpoints and the four sets of 5 post-calibration reach

238   endpoints) and between-participant factor "group" (Mismatch and Veridical). For a significant

239   interaction, paired-sample t-tests were performed within each group, comparing the last set of pre-

240   calibration reaches with each set of post-calibration reaches.

241

242   For the Mismatch group only, the magnitude of change in reach endpoint (first set of post-calibration

243   reaches minus last set of pre-calibration reaches) was compared to the magnitude of proprioceptive

244   recalibration (Δh_P) and the magnitude of total recalibration ($\Delta h_P + \Delta h_V$) in a one-way repeated measures

245   ANOVA. For a significant effect, change in reach endpoint was compared to the other two magnitudes

246   with a paired-sample t-test.

247

248   For the post-hoc t-tests, false discovery rate was controlled by the Benjamini-Hochberg procedure (31)

249   with α set to 0.05. In the text, adjusted p-values are indicated as p_{adj}. Data and analysis code are publicly

250   available at https://osf.io/zy49x/.

251

3. RESULTS

On average, participants in the Mismatch group recalibrated proprioception 17.4 ± 4.0 mm and vision 38.1 ± 6.1 mm (mean $\pm$ SE) in response to a gradually-imposed 70 mm mismatch between visual and proprioceptive cues. The example participant in Fig. 2 recalibrated to a degree consistent with the group behavior. After exposure to the cue conflict, this participant reached shorter distances with the recalibrated hand, consistent with predictions (Fig. 1C); however, this was only evident in the first set of 5 trials post-mismatch (Fig. 2C).

Participants' average reach distances on the four sets of five right-handed reaches (Fig. 3i and iii) were analyzed with a mixed-model ANOVA with factors Group (Mismatch, Veridical) and Reach Set (5 sets) (Fig. 4). There was a significant Reach Set x Group interaction ($F_{4,120} = 2.81$, $p = 0.028$, $\eta_p^2 = 0.008$), suggesting that the two groups differed in reach distance across the five reach sets. There was also an effect of Reach Set on reach distance ($F_{4,120} = 3.97$, $p = 0.0046$, $\eta_p^2 = 0.01$), but no main effect of Group ($F_{1,120} = 0.19$, $p = 0.66$, $\eta_p^2 = 0.006$).

Within each group, paired-sample t-tests were used to compare each set of post-calibration reaches (Fig. 3iii) with the pre-calibration reach set (Fig. 3i). For the Mismatch group, the first and second set of post-calibration task reaches were significantly different from the pre-calibration set ($t_{15} = 3.47$, $p_{adj} = 0.014$; $t_{15} = 2.86$, $p_{adj} = 0.024$). The third and fourth set were not significantly different from the pre-calibration reaches ($t_{15} = 1.52$, $p_{adj} = 0.20$; $t_{15} = 0.76$, $p_{adj} = 0.46$), suggesting any effect of mismatch on reach distance did not last beyond the first two sets of 5 reaches. For the Veridical group, none of the post-calibration task sets of reaches differed significantly from the pre-calibration set (all $p > 0.5$). Finally, comparing the pre-calibration reaches across groups did not yield any evidence that the two groups reached different distances prior to the calibration task ($t_{30} = 0.26$, $p = 0.80$).

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275   For the mismatch group, we compared participants' change in right-hand reach undershoot from the

276   last 5 pre-calibration reaches to the first 5 post-calibration reaches with total recalibration magnitude

277   (visual plus proprioceptive) and with proprioceptive recalibration (Fig. 5). Change in reach undershoot

278   was significantly smaller than total recalibration (t_{15} = -4.32 p_{adj} = 0.0012), but not significantly different

279   from proprioceptive recalibration (t_{15} = 0.46, p = 0.65). This could indicate that change in reach

280   performance does not reflect the sum of visual and proprioceptive recalibration (Fig. 1C), although other

281   interpretations are possible.

283   Participants were questioned about their experience at the conclusion of the session. Most participants

284   did not perceive any forward mismatch between the visual and proprioceptive targets during the

285   calibration task. Two participants in each group reported perceiving such a mismatch, which is

286   consistent with our previous work (7). Participants were also asked to rate their quality of sleep the

287   previous night, their level of attention during the task, and how fatigued they felt after the task, on a

288   scale of 1 to 10. We found no indication that these might differ across groups. Sleep was rated 6.9 ± 1.0

289   (mean ± 95% CI) by the Mismatch group and 6.6 ± 0.8 by the veridical group. Attention was rated 7.2 ±

290   0.5 by the Mismatch group and 7.8 ± 0.6 by the veridical group. Fatigue was rated 4.1 ± 1.4 by the

291   Mismatch group and 3.8 ± 0.8 by the veridical group.

294   **4.   DISCUSSION**

296   Here we asked whether reaching movements show evidence of change after visuo-proprioceptive

297   recalibration in hand position estimates. The Mismatch group, after exposure to a gradual 70 mm visuo-

298   proprioceptive mismatch, made significantly shorter reaching movements. The magnitude of change in

299   reach distance was similar to the magnitude of proprioceptive recalibration. However, reaching

300   performance returned to baseline levels after only 10 reaches. The Veridical group, after exposure to

301   veridically-aligned visual and proprioceptive cues about the hand, showed no evidence of a change in

302   reach distance. Taken together, these results suggest that visuo-proprioceptive recalibration of hand

303   estimates does affect reaching movements, but only briefly.

304

305   **Reach distance affected by visuo-proprioceptive recalibration**

306   We predicted that reach distance would shorten after exposure to a 70 mm forward displacement of

307   visual cues from proprioceptive cues about the hand. We reasoned that with this direction of cue

308   conflict, proprioceptive recalibration would be expected in the forward direction. In other words,

309   participants would come to feel that their target hand was further forward than it actually was. They

310   would then execute reaches of smaller magnitudes, feeling there was less distance to travel from their

311   proprioceptively-perceived hand position to the visual target. Results of the present study support this

312   prediction. The Mismatch group reached shorter distances after exposure to the visuo-proprioceptive

313   mismatch, compared to baseline. Importantly, the Veridical group showed no change in reaching after

314   exposure to veridical visuo-proprioceptive cues, indicating that the reach distance change was specific

315   to the experience of a visuo-proprioceptive cue conflict. Subjects tended to overshoot the reaching

316   target in both groups. This may be related to the lack of visual feedback about hand position at reach

317   initiation, which is known to bias reaching (32,33).

318   There may be more than one mechanism by which recalibration could alter reaching movements. Sober

319   and Sabes (2003, 2005) demonstrated that visual cues predominate for planning a movement vector in

320   extrinsic space, but proprioceptive cues dominate in converting the movement vector to a motor

321   command in joint space (34,35). However, this assumes that visual cues of the hand's starting position

322   are available for planning the movement vector. In the present study there was no visual cue about the

323   hand's starting position in the reaching trials, so coordinate transformations could not be avoided and

324   proprioceptive cues had to be used in computing the movement vector: With the unseen hand

325   positioned at the unseen starting position, subjects had to use their (forward-shifted) proprioceptive

326   estimate of hand position to plan the movement vector to the visual target. In other words, the present

327   results are consistent with perceptual recalibration causing a change in movement vector planning. We

328   have no reason to think anything changed about how the muscle/joint level commands were

329   determined, although we did not test this explicitly.

330

331   An important question to consider is whether it is possible that the reaching hand experienced motor

332   adaptation during the calibration task, or any other motor learning process that could affect reach

333   distance; this would confound our interpretation of the role of proprioceptive recalibration in the

334   change in reach distance. Importantly, the calibration task was designed to preclude any such confound:

335   participants never received any information about where their indicator finger landed in relation to the

336   target, so there was no error signal that could drive motor adaptation. In addition, participants were

337   explicitly instructed to place their indicator finger at the perceived target location, with no time

338   constraints. The one form of motor learning that should be possible in these conditions is for the

339   indicator finger's pointing movements to become less variable across the calibration task. In other

340   words, if the participant executes a movement of their indicator finger and proprioceptive feedback

341   from the indicator hand suggests the finger did not land in the planned position, the brain could fine-

342   tune the motor command to make more accurate predictions. However, this form of learning should not

343   be considered a confound, as it would occur similarly in both the Misaligned and Veridical groups.

344

345   We hypothesized that in the absence of visual feedback about the hand during reaching, only the

346   proprioceptive recalibration would contribute to target undershoot. However, we also considered the

347   possibility that recalibration of visual estimates of the hand could include everything in the visual scene.

348   In other words, it is possible that when visual recalibration occurs, people interpret that as the visual

349 scene being closer than it looks, rather than specifically visual information about the hand. If that were

350 the case, we would expect change in reach undershoot to be larger than proprioceptive recalibration,

351 and more similar to total recalibration, which it was not. On the other hand, given the present study

352 design of shifting cue forward for the Misaligned group, one may wonder if some part of visual target

353 undershoot can be attributed to participant "laziness" or disinclination to point further away with their

354 indicator hand. If so, it would inflate our estimate of total recalibration. If this were the case, we would

355 expect greater undershoot at the smooth target position, which was 40 mm forward of the rough target

356 position, but we previously found that undershoot was nearly identical at the two target positions (36).

357 Regardless, our primary conclusion that perceptual recalibration affects the (same or different)

358 sensorimotor map used for reaching does not depend on the exact quantitative values of perceptual

359 shift or reach shortening. Rather, it is based on the shortened distance of no-feedback reaches that

360 developed in the Mismatch but not the Veridical group; reach shortening is the predicted direction of

361 change whether caused by proprioceptive recalibration, visual recalibration, or both.

362

363 **Reach distance reduction was transient**

364 It is interesting to note that the reduction in reach distance was no longer detectable after only 10

365 reaches. Motor adaptation, in contrast, can be retained even after a year (37). Proprioceptive

366 recalibration that results from motor adaptation can, itself, still be evident after 24 hours (38,39). There

367 are several possible interpretations of this difference. First, more exposure to a visuo-proprioceptive

368 mismatch might result in longer-lasting reduction in reach distance; there were only 42 visuo-

369 proprioceptive exposure trials in the present study, while motor adaptation studies frequently involve

370 hundreds of trials. Second, perhaps the active movement stimulates proprioceptors in a way that

371 overrides proprioceptive recalibration generated at a static position. This possibility could be considered

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372 consistent with RHI studies that found the illusion is reduced by active movement of the stimulated

373 hand (12).

374 It is also possible that proprioceptive recalibration, induced with only a cue conflict and not motor

375 adaptation, is itself transient, so effects on reach distance are also transient. However, evidence

376 suggests that proprioceptive recalibration induced with a cue conflict is robustly retained 24 hours later

377 (36). In an experiment where visuo-proprioceptive recalibration was elicited similarly to the present

378 study, short-term retention of proprioceptive recalibration was partially disrupted after one minute of

379 circle tracing (one circle per second) with the recalibrated finger and 4 minutes of rest; on average,

380 proprioceptive recalibration was reduced 38% by this intervention (36). In the present study, if the

381 transience of reach undershoot is due to proprioceptive recalibration being equally transient, it would

382 mean that proprioceptive recalibration was 100% lost within 10 no-feedback reaches. Given the findings

383 of Wali et al. (2023), we consider it more likely that substantial proprioceptive recalibration remains

384 even after reach undershoot has worn off. If indeed proprioceptive recalibration lasts longer than 10

385 reach trials, it is possible the effect on reach distance does not. This would be consistent with the

386 involvement of multiple body representations: proprioceptive recalibration might occur in the body

387 image, which only briefly interacts with the body schema used to plan reaches. Indeed, different body

388 representations have been associated with different dynamics and timescales (14). Of course, these

389 possible interpretations are not mutually exclusive. Further studies are needed to better understand

390 what factors influence the time course of visuo-proprioceptive recalibration effects on movement.

391

392 **Implications for the sensorimotor map and other body representations**

393 Our prediction of shortened reach distance after visuo-proprioceptive recalibration was based on the

394 idea that perception of body parts is closely linked to motor control, and that reach planning would

395 therefore take into account any changes in perceived hand position in order to maintain movement

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396   accuracy. Consistent with this idea, we have previously observed changes in the excitability of primary

397   motor cortex (M1) that were specifically related to visuo-proprioceptive recalibration, after controlling

398   for motor behavior (11). Furthermore, M1 changes were somatotopically focal, limited to the M1

399   representation of the finger that experienced visuo-proprioceptive cue conflict (10). Findings like these

400   are suggestive of a close relationship between perception of hand position and motor execution

401   involving that hand.

402

403   On the other hand, there is evidence to suggest that changes in perceived hand position may affect a

404   body representation that functions separately from the body representation used to control movement.

405   Paillard (1999) refers to these representations as the body image and the body schema, respectively,

406   based on a double dissociation observed in neuropsychological patients (13). In other words, some

407   patients can correctly use information about their body positioning to move (intact body schema), but

408   do not correctly perceive their body positioning (disrupted body image), while others have the opposite

409   problem (13). This allows us to infer that there are at least two dissociable body representations,

410   although some have suggested that body image should be further divided (12,14).

411

412   The literature includes examples where a perceptual manipulation clearly does not affects motor

413   performance (12), examples where it clearly does (8,22), and also gray areas (15). Some of this literature

414   uses the Rubber Hand Illusion (RHI), in which synchronous stroking of a seen fake arm and the felt real

415   arm creates the illusion of body ownership over the fake arm (15). Kammers et al. (2009) found that

416   perceptual bodily judgments were sensitive to the RHI, but ballistic motor responses were not. The

417   authors thus concluded that the illusion affected the body image, but not the body schema (12).

418   However, while the RHI entails a visuo-proprioceptive discrepancy like the present study, there are also

419   important differences to be considered. Our paradigm lacks synchronous tactile stimulation, and the

420   visual stimulus is reduced to a disembodied white disc. The RHI is associated with "visual capture",

421   where the visual signal is so much stronger than the proprioceptive signal that most recalibration is

422   likely proprioceptive rather than visual. In contrast, our paradigm is associated with a slightly stronger

423   weight of proprioception compared to vision, and greater visual recalibration than proprioceptive

424   (40,41). Indeed, Kammers et al. (2009) suggested that weighting of vision vs. proprioception in

425   multisensory integration could explain their results, with perceptual judgments relying heavily on vision

426   and ballistic movements relying on proprioception.

427

428   Even within the RHI literature, there are grey areas in terms of which body representation appears

429   affected. Kammers et al. (2009) noted that the classic RHI study by Botvinick and Cohen (1998) assessed

430   illusion strength by asking participants to make pointing movements to where they perceived their other

431   hand. The pointing movements were clearly sensitive to the illusion (15), unlike the ballistic movements

432   used by Kammers et al. (2009). However, the pointing movements may have accessed a perceptual

433   judgment in a way that ballistic movements do not (12).

434

435   On the other end of the spectrum, there is evidence that exposure to a visuo-proprioceptive mismatch

436   in a cursor rotation task robustly affects reaching movement (8,22). The cursor rotation paradigm is

437   often used to elicit visuomotor adaptation: participants move to a visual target while the corresponding

438   cursor deviates by some angular magnitude. This results in systematic movement errors, which are

439   reduced by trial-and-error adaptation of the motor command. Proprioceptive recalibration also occurs,

440   due to both sensory prediction errors and the cross-sensory mismatch created by the deviation of the

441   cursor from true hand position (21). Salomonczyk et al. (2013) modified the cursor rotation paradigm to

442   remove the movement errors that could drive visuomotor adaptation; instead, participants moved their

443   hand actively or passively along a set channel that was gradually deviated from the cursor, which always

444   went straight to the target. After this exposure, participants made self-guided reaches with no cursor.

445   These no-cursor reaches showed a directional change after exposure to the visuo-proprioceptive

446   mismatch, and the change in reach direction was correlated with participants' magnitude of

447   proprioceptive recalibration (8). In fact, Tsay et al. (2022) recently suggested that these types of results

448   support the idea of implicit motor adaptation being driven by proprioceptive recalibration, not the other

449   way around (42). We checked our Mismatch group for a correlation between proprioceptive

450   recalibration and change in reach distance, as an exploratory analysis, but there was no association ($r <$

451   0.1). A sample of 16 is too small to definitively answer this question (43), but it would be valuable to

452   examine such individual differences in a larger study.

453

454   While a visuo-proprioceptive mismatch created in the context of cursor rotation seems to clearly alter

455   the body schema, it is difficult to generalize such findings to visuo-proprioceptive recalibration in

456   general, which does not require either active or passive movement, or even a reaching target. The

457   nature of a cursor rotation is that it exists in the context of target-directed movement: there is no visuo-

458   proprioceptive mismatch at the home position, and the mismatch linearly increases as the person

459   approaches the target. In addition, the mismatch is applied in body-centered coordinates; moving the

460   hand to the right would result in a mismatch of the opposite direction in extrinsic space compared to

461   moving the hand to the left. In contrast, the present study imposed the mismatch with the hand

462   positioned in a static location, and that hand made no movements toward a target while the mismatch

463   was imposed.

464

465   In sum, the present paradigm has features in common with both the RHI and the cursor rotation task,

466   but also features that differ. Based on the above studies, we would suggest that our visuo-

467   proprioceptive mismatch task affected primarily the body image, as participants were explicitly asked to

19

468   indicate their perceived positions of static hand targets as accurately as possible without regard to

469   speed (12,15). The straight-ahead reaches presumably accessed the body schema, which makes it

470   surprising that we observed a shortening of reaches. However, it should be noted that the body schema

471   and body image likely interact with each other (14), making it challenging to draw more specific

472   conclusions.

473

474   **Conclusions**

475   We predicted that straight-ahead reach distance would shorten after exposure to a forward

476   displacement of visual cues from proprioceptive cues about the hand, which leads to proprioceptive

477   recalibration in the forward direction. Results support this prediction, but the reduction of reach

478   distance was transient. This is consistent with some degree of separation between body representations

479   for perception and action.

480

481
482   **CRediT author statement**

483   HJB: Conceptualization, Methodology, Software, Formal analysis, Writing – Review & Editing,

484   Visualization, Supervision, Funding acquisition.

485   YL: Software, Formal analysis, Investigation, Writing – Original Draft, Visualization.

486

489

490   **Endnote**

491 At the request of the authors, readers are herein alerted to the fact that additional materials related to

492 this manuscript may be found at https://osf.io/zy49x/. These materials are not a part of this manuscript

493 and have not undergone peer review by the American Physiological Society (APS). APS and the journal

494 editors take no responsibility for these materials, for the website address, or for any links to or from it.

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592   **Figure captions**

593
594   **Figure 1.** Top row: Participant holds handle of robotic manipulandum in right hand. Images viewed in

595   mirror of 2D VR display appear to be in line with top of manipulandum handle. Not pictured: fabric

596   preventing vision of the upper arms. No direct vision of hands is possible. **A. Pre-calibration reaches**.

597   Participant performs straight-ahead reaching with no visual feedback about hand position, stopping at

598   perceived position of visual target. The hand was brought passively back to the invisible starting position

599   after each trial. **B. Visuo-proprioceptive calibration. i.** Participants use their left index finger on a

600   touchscreen to indicate the perceived position of visual (V), proprioceptive (P), and combined (VP)

601   targets. No performance feedback or knowledge of results was available at any time. For the Veridical

602   group, VP targets remained veridical throughout. **ii.** For the Mismatch group, the visual component

603   (white disc) gradually shifted forward to a maximum of 70 mm. This generally results in both

604   proprioceptive recalibration toward the visual target (Δh_P) and the visual recalibration toward the

605   proprioceptive target (Δh_V). Transparent hands and writing were not visible to participants. **C. Post-**

606   **calibration reaches.** Same procedure as pre-calibration reaches. **i-ii.** For the Mismatch group, if Δh_P

607   affects reaching, we predict participants will stop short of the visual target because they feel their hand

608   is further from them (closer to the target) than it is. With only proprioceptive information about hand

609   position, planned movements (red dashed lines) should be shorter relative to pre-perturbation (black

610   arrow) for the Mismatch group but not the Veridical group.

611
612   **Figure 2**. Example participant in the Mismatch group. **A.** Pre-mismatch reaches. Movement paths of the

613   5 right-handed reaches immediately preceding mismatch task. With no performance feedback or

614   knowledge of results, this participant consistently overshot the reach target (grey bar). **B.** The mismatch

615   task gradually imposed 70 mm of visuo-proprioceptive mismatch by shifting the white disc (V target)

616   forward from the stationary right hand (P target). This participant recalibrated both proprioception (Δh_P

617   = 29.6 mm) and vision (Δh_V = 28.9 mm). **C.** Four sets of 5 right-handed reaches following mismatch task.

618   The first set of 5 reaches undershot the pre-mismatch mean (dashed line) by 16.4 mm.

619   **Figure 3.** Group reaching distances pre- and post-calibration task. **A. Mismatch group (N=16). i.** Mean

620   distance of the 5 right-handed reaches immediately preceding calibration task. Dots represent individual

621   participants. Reaches started at 0 mm and the target was at 100 mm. **ii.** Mismatch task. Participants

622   pointed with their left indicator finger to P targets (right hand, dashed grey line), V targets (white disc,

623   solid grey line), and VP targets (combined), with a 70 mm mismatch gradually imposed. On average,

624   participants recalibrated both vision and proprioception *(Δh_V = 38.1 mm, Δh_P = 17.4 mm)*. **iii.** Mean

625   distance of the five sets of 5 right-handed reaches immediately following the calibration task. *First and

626   second sets of 5 reaches were significantly different from the pre-calibration task reaches (p_{adj} < 0.05). **B.**

627   **Veridical group (N=16).** Post-calibration reaches did not differ significantly from pre-calibration task

628   reaches. All error bars and shaded regions represent standard error.

629

630   **Figure 4.** Interaction plot of reach distance across reach sets in the Mismatch vs. Veridical groups. Reach

631   set 1 corresponds to the 5 pre-calibration task reaches. Reach sets 2-5 correspond to the four sets of 5

632   post-calibration reaches.

633

634   **Figure 5**. In the Mismatch group, reach undershoot changed by an average magnitude of 20.9 mm in the

635   predicted direction. This magnitude was significantly smaller than the total magnitude of recalibration

636   (visual plus proprioceptive), which averaged 55.5mm (*p_{adj} < 0.05). Change in reach undershoot did not

637   differ significantly from the magnitude of proprioceptive recalibration, which averaged 17.4 mm.

638